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### **Reinterpreting the relationship between number of species and number of links connects community structure and stability**

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## Title

Reinterpreting the relationship between number of species and number of links connects community structure and stability

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## Abstract

**For 50 years, ecologists have examined how the number of interactions (links) scales with the number of species in ecological networks. Here, we show that the way the number of links varies when species are sequentially removed from a community is fully defined by a single parameter identifiable from empirical data. We mathematically demonstrate that this parameter is network-specific and connects local stability and robustness, establishing a formal connection between community structure and two prime stability concepts. Importantly, this connection highlights a local stability-robustness trade-off, which is stronger in mutualistic than in trophic networks. Analysis of 435 empirical networks confirmed these results. We finally show how our network-specific approach relates to the classical across-network approach found in literature. Taken together, our results elucidate one of the intricate relationships between network structure and stability in community networks.**

## Main text

Understanding which properties of ecosystems determine their response to disturbances has become a central question for ecologists. Such disturbances can have various effects on ecosystems – going from infinitesimal changes in species densities to species loss. The former case has been studied mostly through local stability analysis<sup>1</sup>, which labels a community as stable when it returns to its equilibrium after a pulse disturbance of species densities. Local stability – measured with the real part of the dominant eigenvalue of the community matrix – has been shown to be impacted by numerous ecosystem properties<sup>1–5</sup>, the simplest being the number of species  $S$  and the number of links  $L$  between them<sup>6</sup>.

These two structural properties,  $S$  and  $L$ , are known to also impact community robustness, which is usually defined as the fraction of species one needs to remove from a community in order to lose 50% of the original species richness<sup>7,8</sup>. This fraction is, in theoretical studies, computed through *in-silico* extinction experiments: because species are interconnected, the removal of one of them might cascade into further extinctions. Such extinctions occur when a species is left without any resource<sup>7–10</sup> or mutualistic partner<sup>11,12</sup>, which is less likely to happen when a community is well connected<sup>7,10</sup>. We therefore predict that local stability and robustness are negatively interrelated<sup>13</sup>. There is, however, no formal test of this intuition in the current literature, as most studies tend to focus on one component of community stability only<sup>14</sup>.

The local stability-robustness relationship is further complicated by the fact that  $L$  and  $S$  are also interrelated. The  $L \sim S$  relationship has been described since the 1980s as  $L = a \cdot S^b$ , where  $a$  and  $b$  are constants<sup>15,16</sup>. A dominant approach to estimate the value of these constants has been to consider the  $L \sim S$  relationship as universal<sup>16–18</sup>: by computing the  $L$  and  $S$  of multiple communities, ones should be able to estimate a single  $a$  and  $b$  via linear regression in the  $\log(L) \sim \log(S)$  space<sup>15–24</sup>. However, this approach has led to various values of  $a$  and  $b$  and, therefore, to various  $L \sim S$  relationships ranging from a linear<sup>15</sup> ( $b = 1$ ) to a quadratic<sup>16</sup> ( $b = 2$ )

function. Indeed, several factors such as interaction type<sup>4,25</sup>, environmental constancy<sup>5,26,27</sup>, habitat type<sup>28</sup> or spatial scale<sup>29,30</sup> affect the value of  $b$ . This variation confirms early work suggesting that the  $L \sim S$  relationship might in fact be a community-specific property<sup>15,22</sup>. In that case, each community would have a specific  $L \sim S$  curve and temporal (or spatial) variations of  $S$  would move the community along this curve<sup>22</sup>.

Here, we reinterpret the  $L \sim S$  relationship as a system-specific characteristic and, by doing so, discover a structural property that can be easily inferred from empirical data. A key result is that this structural property formally predicts both the robustness and local stability of biological networks, imposing a trade-off between these two stability properties. We extract this structural property from 186 trophic and 249 mutualistic networks taken from the literature and public databases, confirming our analytical results and showing that the local stability-robustness trade-off is stronger in mutualistic than in trophic networks.

## Results

We begin by introducing the idea of a network-specific  $L \sim S$  relationship using *in-silico* extinction experiments. We sequentially and randomly remove species (one at a time) from one network and count the number of species (i.e. size) and the number of links (i.e. edges) of this network after each removal, until there are no species left. A secondary extinction occurs when a species has no resource or mutualistic partner left (for the species having initially in- and outgoing links) or when they are isolated (i.e. left without any links, for the species having initially no incoming links). This random decomposition, when repeated multiple times, yields pairwise observations of  $L$  and  $S$  for a given network, and therefore a network-specific  $L \sim S$  relationship (Fig. 1). A power law describes this relationship:  $L = a \cdot S^b$ , where  $a$  and  $b$  are network-specific (see Supplementary Equations 1 for a demonstration). The value of  $a$  and  $b$  can be computed through regression in the  $\log(L) \sim \log(S)$  space, with  $\log(a)$  being the

intercept of this relationship, and  $b$  its slope (Fig. 1). We applied this approach to predict network-specific  $L \sim S$  relationships for empirical networks ( $\overline{R^2} \geq 0.99$ , Extended Data Figure 1). However, this method gives little theoretical insight into community structure and requires simulating the entire decomposition process for each network, which is fastidious and time consuming.

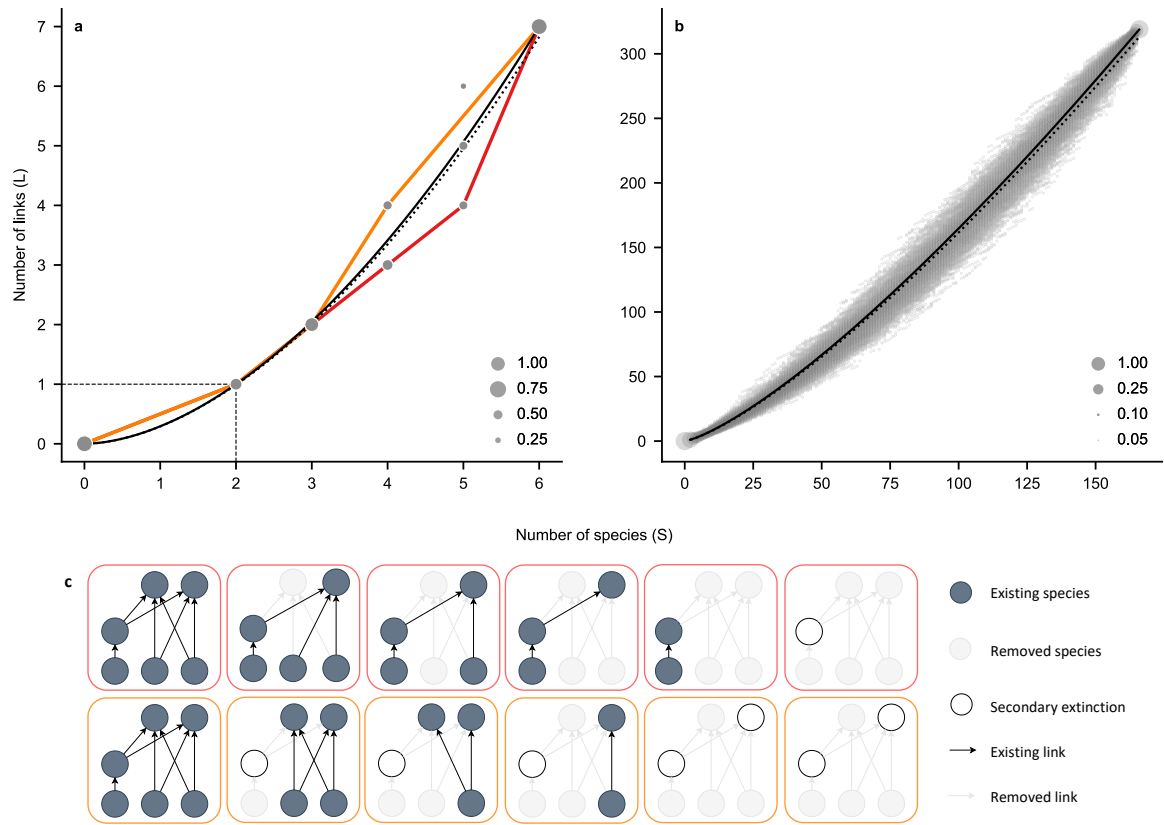
To overcome this, we want to relate the values of  $a$  and  $b$  to one another. Since our rule for secondary extinctions prohibits the persistence of isolated species (relaxation of this rule is explored later), a network consisting of only two species should have exactly one link: if  $S = 2$  then  $L = 1$ . This would imply that  $a = 2^{-b}$ . Thus, one parameter ( $b$ ) would fully characterize the  $L \sim S$  relationship of a community network:

$$L = \left(\frac{S}{2}\right)^b \quad (1)$$

Given the  $L$  and  $S$  of the initial network (i.e. before any species removal), we can compute  $b$  as:

$$b = \frac{\log_2(L)}{\log_2(S) - 1} \quad (2)$$

This value can be used in Equation 1 to predict how  $L$  changes along the network's decomposition (Fig. 1). Remarkably, this single-parameter model predicts the  $L \sim S$  relationship as accurately as the two-parameter log-log regression model ( $\overline{R^2} \geq 0.96$ , Extended Data Figure 1). Equations 1-2 therefore describe the network-specific relationship between  $L$  and  $S$  without the need to simulate network decomposition; the initial network suffices to compute  $b$  and, therefore, the whole decomposition process.



**Figure 1 | The network-specific link-species relationship in two empirical networks.** (a) Decomposition of the Lake Crescent trophic network<sup>58</sup>: the initial network has 6 species and 7 links. Each dot represents the network after the removal of a number of species; the likelihood of reaching each dot in the  $L \sim S$  plane is represented by its size. Black lines are the predicted  $L \sim S$  relationship based on the log-log regression parameters (dotted line,  $a = 0.29$ ,  $b = 1.76$ ,  $R^2 = 0.988$ ) and on Equation 1 (solid line, with  $b = \log_2(7)/(\log_2(6) - 1) = 1.77$ ,  $R^2 = 0.976$ ). The orange and red lines are two examples of network decompositions: while the red line represents the least frequently observed trajectory (3% of the *in-silico* extinction experiments), the orange one is the most observed trajectory (22%). (b) Decomposition of the plant-pollinator network of the Mt Murray<sup>59</sup>: the initial network has 166 species and 319 links. The predictions based on the log-log regression (dotted line,  $a = 0.39$ ,  $b = 1.31$ ) and on Equation 1 (solid line,  $b = 1.30$ ) lead to an  $R^2$  of 0.996 and 0.992, respectively. (c) Example of decomposition process leading to the red (top) and orange (bottom) lines of panel (a).

Since  $b$  predicts the decomposition of a specific network, it contains information about the consequences of species removal. These can be expressed as the average number of species lost  $\widehat{\Delta S}$  when one species is removed (e.g.  $\widehat{\Delta S} = 1$  when there is no secondary extinction). This average is the slope of the relationship between the number  $n$  of species lost after the removal of a number  $r$  of species (Fig. 2a-b):

$$n = \widehat{\Delta S} \cdot r \quad (3)$$

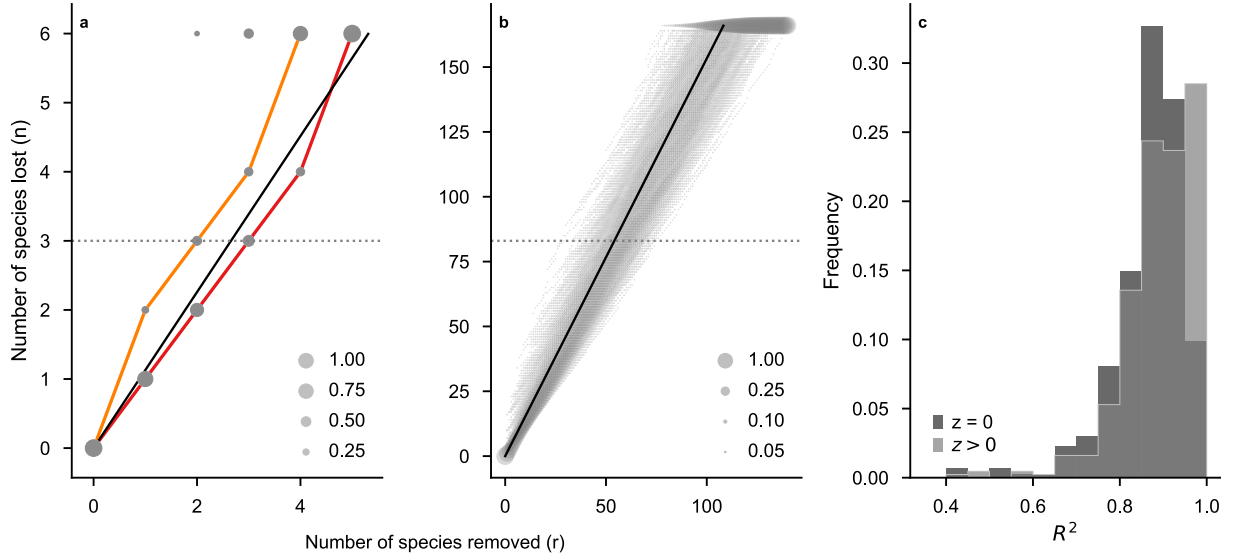
For  $\widehat{\Delta S}/S$  sufficiently small, the following equation allows approximation of  $\widehat{\Delta S}$  (Supplementary Equations 2):

$$\frac{\widehat{\Delta L}}{\widehat{\Delta S}} \approx b \cdot \frac{L}{S} \quad (3b)$$

where  $\widehat{\Delta L}$  is the mean number of links lost when one species is removed and equals the mean degree of the network: when a species is removed, the number of links lost is its number of in- and outgoing links. Therefore,  $\widehat{\Delta L} = 2 \cdot L/S$ . Replacing  $\widehat{\Delta L}$  in Equation 3b results in  $\widehat{\Delta S} \approx 2/b$ . This approximation of  $\widehat{\Delta S}$  holds true if we consider that all species might experience secondary extinctions. However, some species ("independent species" hereafter) might not undergo such extinctions (e.g. a prey might not depend on its predator for its survival, some plants might self-reproduce, etc.). To take this into account, we define  $z$  as the probability that a randomly-chosen species does not undergo secondary extinction: the number of species lost when one species is removed is 1 with the probability  $z$  and  $2/b$  with a probability  $(1 - z)$ . Therefore:

$$\widehat{\Delta S} \approx (1 - z) \cdot \frac{2}{b} + z \quad (4)$$

To test the effect of  $z$  on  $\widehat{\Delta S}$ , we computed  $\widehat{\Delta S}$  for the empirical networks following two scenarios: (1) all species can undergo secondary extinction ( $z = 0$ ); (2) species having no incoming links are considered as independent<sup>7,8,31,32</sup> (i.e.  $z$  equals the fraction of basal species in trophic network and of plants in mutualistic ones). Note that scenario (1) aligns with the assumption on which Equations 1-2 are built (isolated species are considered as extinct), while scenario (2) does not. Nevertheless, Equations 1-2 describe the network-specific  $L \sim S$  relationship in both scenarios (Extended Data Figure 2). Consequently, Equation 4 predicts the number of species lost after removing a defined number of species in all *in-silico* extinction experiments (Fig. 2c,  $\overline{R^2} = 0.87$  and  $0.89$  in the first and second scenario, respectively).



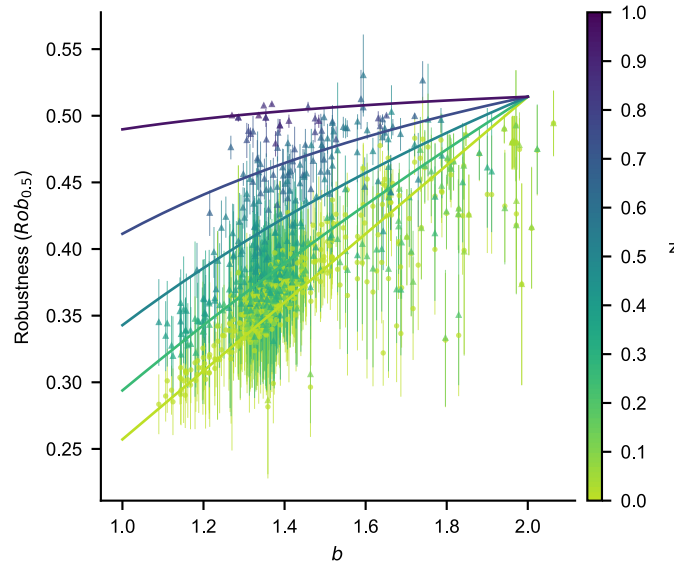
**Figure 2 | Prediction of the number of species lost based on the number of species removed.** (a-b) Relationship between the number of species removed  $r$  (primary extinction) and the number of species lost  $n$  (primary + higher order extinctions) obtained through network decomposition without independent species ( $z = 0$ ) for the example of the Lake Crescent trophic network<sup>58</sup> (a) and the Mt Murray plant-pollinator network<sup>59</sup> (b). Dot size indicates the likelihood of each observation across 10,000 *in-silico* experiments. The solid black line corresponds to the  $n = \widehat{\Delta S} \cdot r$  relationship, with  $\widehat{\Delta S}$  given by Equation 4 ( $R^2 = 0.838$  in (a) and  $0.924$  in (b)); the dotted horizontal lines indicate the loss of 50% of the species. On panel (a), the orange and red lines correspond to the decomposition examples given in Figure 1c. (c) Distribution of the  $R^2$  (bin width = 0.05) computed for the 435 empirical networks, comparing the predicted numbers of species lost (Equation 3 with  $\widehat{\Delta S}$  computed based on Equation 4) with the observations obtained through the *in-silico* experiment following the first (dark grey,  $z = 0$ ) or the second (light grey,  $z > 0$ ) scenario.

Because  $b$  allows predicting the number of species lost for a defined number of species removed, one can express community robustness as a function of  $b$  (and  $z$ ). Indeed, robustness can be defined as the fraction of species one needs to remove from a network in order to lose a fraction  $x$  of all its species<sup>7,8</sup>. This definition can be formalised via the number  $r$  of randomly-chosen species to remove such that  $x \cdot S$  is the total number of species lost on average (when  $S$  is large, see Methods):  $x \cdot S = \widehat{\Delta S} \cdot r$ . Knowing this, defining robustness as  $r/S$  leads to  $Rob_x = x / \widehat{\Delta S}$ . Combining this with Equation 4, we obtain a formal expression for community robustness:

$$Rob_x = \frac{x}{\left( (1 - z) \cdot \frac{2}{b} + z \right)} \quad (5)$$



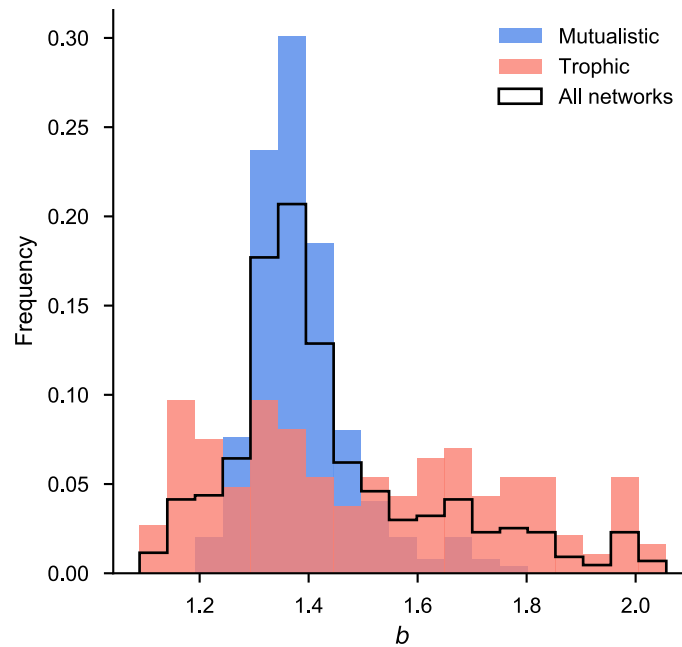
Equation 5 matches simulated robustness obtained through the *in-silico* extinction experiments (Fig. 3,  $R^2 \geq 0.61$  for the most commonly used fraction of  $x = 50\%$ <sup>7,8</sup>; for other fractions see Extended Data Figure 3).



**Figure 3 | Robustness (averaged  $\text{Rob}_{0.5}$  over 10,000 simulations) of 435 empirical networks and its prediction based on the parameter  $b$  shaping the link-species relationship.** Circles indicate the robustness when every species in the network could potentially be subject to secondary extinctions ( $z = 0$ ,  $R^2 = 0.60$ ), while triangles indicate simulations where independent species are unable to undergo secondary extinctions ( $z > 0$ , with  $z$  being the proportion of species having no incoming links,  $R^2 = 0.73$ ). Error bars show one standard deviation and lines correspond to our analytical predictions (Equation 5 with  $z = 0, 0.25, 0.5, 0.75$  and  $0.95$ ;  $S = 35$ , the median  $S$  across all networks). Values of  $b$  are computed with Equation 2 for each network.

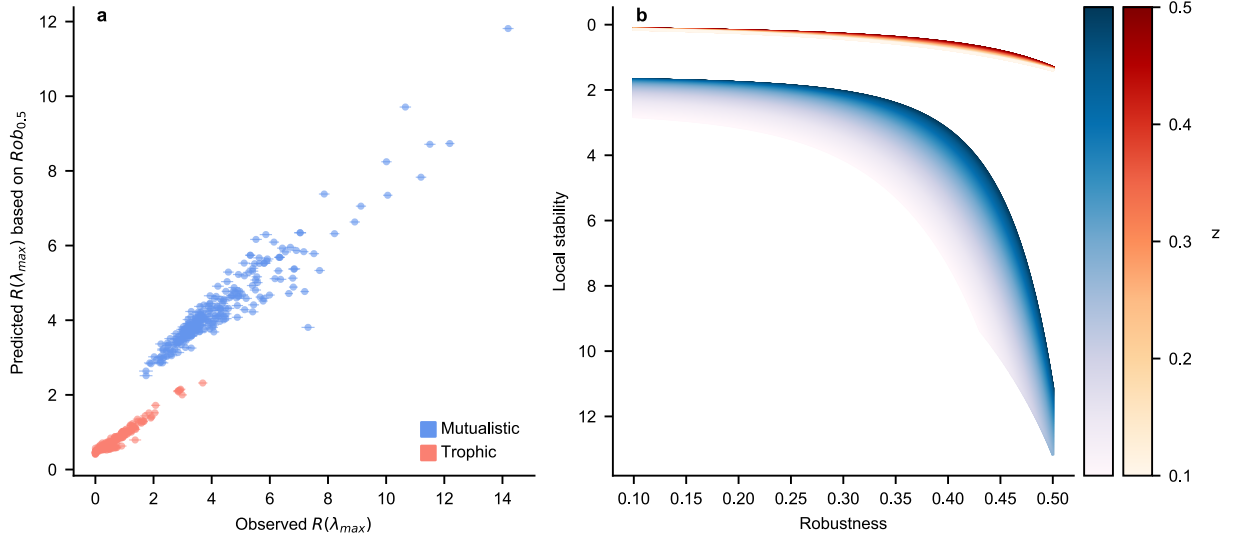
Species removal is an extreme kind of perturbation<sup>31</sup>, and one might want to know how a community responds to less dramatic changes such as infinitesimal changes in species densities. Therefore, we estimated the local stability of each network using the real part of the rightmost eigenvalue ( $\Re(\lambda_{\max})$ ) of its community matrix: lower eigenvalues denote greater stability. We find that the single parameter  $b$  describing the  $L \sim S$  relationship (Equation 2) can be introduced into known equations for  $\Re(\lambda_{\max})$ <sup>2,3</sup> (see Methods). Using these, we can express local stability as a function of  $b$ :  $\Re(\lambda_{\max})$  is proportional to  $(S/2)^{(b-1)}$  in mutualistic networks and to  $(S/2)^{(b-1)/2}$  in trophic ones (Equation 7-8 in Methods). These novel equations match the empirical  $\Re(\lambda_{\max})$ , obtained by entry-wise multiplication of the network's adjacency matrix and random matrices with entries drawn from a half-normal distribution ( $R^2 = 0.80$  and  $0.75$

for mutualistic and trophic networks, respectively; 1,000 random draws per network): everything else being equal,  $b$  has a higher effect on  $\Re(\lambda_{max})$  in mutualistic than in trophic networks. Therefore, one might expect the mean value of  $b$  to be lower in empirical mutualistic networks, which is the case (Fig. 4; Welch test,  $p < 0.001$ , Extended Data Figure 4-5). Furthermore, the variance of  $b$  is lower in mutualistic networks (Fig. 4; Levene test,  $p < 0.001$ , Extended Data Figure 4-5). This can be explained by the fact that, to maintain the local stability unchanged when  $S$  increases, a small decrease of  $b$  is sufficient in mutualistic networks (small  $\text{var}(b)$ ) while a bigger decrease is needed in trophic networks (bigger  $\text{var}(b)$ ). This is confirmed by the fact that the slope of the across-network regression of  $b$  against  $S$  (i.e.  $\text{cov}(\mathbf{S}, \mathbf{b})/\text{var}(\mathbf{S})$ ) is less negative in mutualistic than in trophic networks (-0.0005 and -0.0012, respectively;  $p < 0.001$ ; Extended Data Figure 4-5). We found these results to be robust to changes in sampling effort between both network types using subsampling (Extended Data Figure 4).



**Figure 4 | Distribution of the parameter  $b$  for of the 435 empirical networks used in this study.** The black line indicates the distribution of  $b$  when all networks are considered while the blue histogram corresponds to the distribution of  $b$  in mutualistic networks and the red histogram to the one in trophic networks. The mean value of  $b$  is 1.387 in mutualistic networks and 1.505 in trophic ones; the variances are 0.008 and 0.067, respectively.

Finally, because  $b$  also appears in the robustness equation (Equation 5), one can examine how local stability and robustness relate (Fig. 5). These relationships reveal a trade-off between the two stability measures, this trade-off being stronger in mutualistic than in trophic networks.



**Figure 5 | Prediction of local stability based on robustness for trophic (red) and mutualistic (blue) networks.** (a) Predicted local stability based on robustness (average  $Rob_{0.5}$  over 10,000 decompositions per network, with  $z = 0$ ) compared to the averaged  $\Re(\lambda_{\max})$  over 1,000 random community matrices per network, and this for 186 empirical trophic networks (red,  $R^2 = 0.66$ ) and 249 empirical mutualistic ones (blue,  $R^2 = 0.61$ ). Error bars show one standard deviation. (b) Theoretical relationship between robustness and local stability for various value of  $z$ . As local stability depends on species richness  $S$ , we show theoretical relationship for  $S = 35$ , the median  $S$  across all networks. The red and blue lines are based on the analytical expression of  $\Re(\lambda_{\max})$  for trophic and mutualistic networks, respectively (Equation 7-8 in Methods). Colour shading indicates the proportion of independent species ( $z$ ) in the networks.

Drawing conclusion from sets of networks having different structural properties as we do here is reminiscent of the usual approach used in the literature to describe the relationship between  $L$  and  $S$  across networks (cf. Introduction). In this approach, the relationship between  $L$  and  $S$  is obtained through linear regression in the log-log space performed on a collection of networks having different  $L$ ,  $S$  and  $b$ . Following ordinary least squares, the slope  $\beta$  of this across-network relationship is (see Supplementary Equations 3 for a demonstration):

$$\beta = \bar{b} + \frac{\text{cov}(\log(S)^2, \mathbf{b}) - \text{cov}(\log(S), \mathbf{b})(\log(2) + \overline{\log(S)})}{\text{var}(\log(S))} \quad (6)$$

As said before, the first term of this equation is lower in mutualistic than in trophic networks (cf. averaged  $b$ ) while the second term is higher (cf. slope of  $b \sim S$ ), leading to no significant difference for  $\beta$  between the two interaction types ( $p > 0.001$ ), unless more than 200 networks are taken into account (Extended Data Figure 4-5). Finally, when one samples a very large number of networks with sufficiently different  $S$  (high variance of  $\log(S)$ ),  $\beta$  equals the averaged  $b$ .

## Discussion

We predicted that robustness and local stability should be negatively interrelated because of the way they correlate with community structure. Our results confirm this intuition by formally relating robustness and local stability to a community-specific parameter,  $b$ . The value of this parameter describes how the number of species  $S$  and the number of links  $L$  in a specific community covary as species are sequentially removed from it.

The parameter  $b$  is defined as the exponent of the network-specific power-law between  $L$  and  $S$ . This power-law emerges from the degree distribution of ecological communities (Supplementary Equation 1) and is sufficiently flexible to accommodate for the full range of possible  $L \sim S$  relationships from a network made of specialists only ( $b = 1$ ) to a fully connected network ( $b = 2$ ). Using a power-law, however, implies that the  $L \sim S$  relationship is monotonic. This assumption will be violated when species develop new links to compensate the loss of their prey/partners (rewiring)<sup>33</sup>. Yet, it has been argued before<sup>9</sup> that these adaptive links should be observed at least once when a network is sampled for a sufficient amount of time.

We demonstrated that  $b$  predicts the relationship between the number of species lost ( $n$ ) and the number of species removed ( $r$ ) from a system (Fig.2, Equation 3-4): communities with lower resistance have steeper  $n \sim r$  relationships<sup>7,8,11,12</sup>. The  $n \sim r$  relationship is usually described by the average number of secondary extinctions ( $\widehat{N}_2$ )<sup>34</sup>, the extinction area ( $EA$ )<sup>9,35,36</sup>

or the extinction slope ( $ES$ )<sup>37–40</sup>. While  $\widehat{N}_2$  and  $EA$  were so far estimated based on the results of *in-silico* experiments only, they can now be directly linked to the network structure (because  $\widehat{N}_2 = \widehat{\Delta S} - 1$  and  $EA$  is the integral of Equation 3). The extinction slope, for its part, describes the  $n \sim r$  relationship as a hyperbolic function<sup>37–39</sup>, while we assumed it is linear. This difference is due to the strategy used to remove species from the network<sup>8,41</sup>: while we performed random removals (i.e. errors), other studies have considered "attacks"<sup>42</sup> in which the most connected species is removed at each step of the decomposition. In this latter case,  $n$  increases rapidly with  $r$  before slowly stabilizing. The number of species lost is, therefore, higher when facing attacks than when facing errors<sup>7,8,42</sup>. Some studies also explored the consequences of removing the least connected species. Our results (i.e. random removals) represent an intermediate case<sup>7,11</sup> and therefore reflect the impact of species loss *per se*, without any distinction between species' functionality<sup>41</sup>. However, note that our framework could, in theory, be adapted to predict network decomposition following the two other removal strategies by using the actual value of  $\Delta L$  instead of the mean degree in Equation S2 (Supplementary Equation 2). This adaptation could enhance the applicability of our predictions to anthropogenically-caused species removals, which are often not random<sup>7</sup>. This, however, would require knowledge of the exact degree distribution of the studied network, whereas the approach used here makes it possible to predict the  $n \sim r$  relationship based on  $L$  and  $S$  only (Equations 3-4).

Equation 3-4 highlight the fact that, when a network is more connected (high value of  $b$ ), it resists species removal better (lower  $\widehat{\Delta S}$ ), which is in accordance with studies about the average number of secondary extinctions<sup>34</sup>, extinction area<sup>35</sup> and extinction slope<sup>37</sup>. This result is also in line with the positive relationship between community robustness ( $Rob_{0.5}$ ) and connectance ( $C = 2 \cdot L/S^2$ ) observed in previous studies<sup>7,10,34,35</sup> (but see<sup>43,44</sup>). Robustness and connectance are usually related logarithmically<sup>7,35</sup>. Our analytical expression of  $Rob_{0.5}$  (Equation 5)

confirms this relationship: because  $b$  can be expressed as a function of  $\log(C)$  ( $b = \frac{\log(C \cdot S^2/2)}{\log(S/2)}$ ), so can the robustness ( $Rob_x = (x/2) \cdot \frac{\log(C \cdot S^2/2)}{\log(S/2)}$ , for  $z = 0$ ). To our knowledge, this is the first analytical link between community structure and robustness.

Interestingly, if we assume that all species might undergo secondary extinction ( $z = 0$ ), robustness increases linearly with  $b$  ( $Rob_{0.5} = b/4$ , Fig. 3). Two cases, however, can lead to a non-linear relationship between  $Rob_x$  and  $b$ . A first case is where species do not entirely depend on their neighbours for their survival. We tested this case by using a non-zero value for  $z$  in Equation 5. As an example, we assumed that species having no incoming links are independent (i.e. do not depend on other species for their survival)<sup>7,10,11,31,32,36,45</sup>. Because there is no rewiring, this assumption does not impact the decomposition process itself but only maintains higher richness along the decomposition and leads, therefore, to higher robustness (see Methods). The decomposition is also not affected if we consider species having only incoming links as independent. However, if independent species have in- and outgoing links, they prevent extinction cascades, affecting the decomposition process. Such scenarios are not taken into account in this study but techniques could accommodate these<sup>46</sup>. However, assuming a whole fraction of a network as independent is not representative of reality<sup>12,47-49</sup> and  $z$  should be estimated based on data and prior knowledge. One approach is, for example, to use species life history traits to define an intrinsic demographic dependence on mutualism for a given community<sup>43,44</sup> ( $\propto 1 - z$ ). This approach has shown that, when the intrinsic demographic dependence is lower, robustness is higher<sup>43,44</sup>. These results suggest that, in cases where  $z$  takes realistic values, the positive effect of  $z$  on robustness described by Equation 5 still stands (Fig. 3). A second case where a non-linear relationship between robustness and  $b$  can emerge is the one where species might go extinct when some (as opposed to all) of their resources are extinct. Equation 5 tacitly assumes that species are able to compensate the loss of prey/partners by

interacting more strongly with their remaining prey/partners<sup>7,8,10,11,31</sup>. Relaxing this assumption (by, for example, taking the interaction frequency into account) will lead to more secondary extinctions and, thus, to a lower robustness<sup>34,36,50</sup>. Equation 5 is therefore the best-case scenario<sup>9</sup> without rewiring<sup>32,51</sup> when species are randomly removed.

We linked community robustness to local stability and highlighted a trade-off between these two stability measures (Fig. 5): when a network is well connected, species are able to compensate the loss of their neighbours<sup>7,10,34</sup> but a small change in species densities will propagate further into the network<sup>1,4,5,52</sup>. While this result is quite intuitive, the equations we presented allow a formal reduction of the dimensionality of stability<sup>13</sup>. Interestingly, while one equation suffices to predict robustness for both mutualistic and trophic networks, the local stability of these two interaction types differs in how they relate to community structure<sup>2,3</sup>: when  $S$  increases, a small decrease of  $b$  should allow to maintain local stability in mutualistic networks while a larger decrease of  $b$  would be needed in trophic ones. This will hold true as long as a change in  $S$  does not lead to a change in the mean interaction strength  $\mu$ , their variance  $\sigma$  or correlation  $\rho$ . If, for example,  $\sigma$  decreases when  $S$  increases,  $b$  might stay unchanged. Comparing  $\text{var}(b)$  as well as the slope of the  $b \sim S$  relationship between the two interaction types confirmed the expectation that  $b$  decreases faster with  $S$  in trophic than in mutualistic networks. These results, combined with similar trends found in other studies<sup>4,53</sup> suggest that local stability constrains community structure by imposing a stronger trade-off between  $b$  and  $S$  in trophic networks.

The results we obtained comparing the mean value of  $b$  ( $\overline{b_M} < \overline{b_T}$ ) suggest a lower connectance in mutualistic than trophic networks, which differs from what is proposed in the literature<sup>4,53</sup>. This difference can be due to interaction strengths differences or to dataset size: in our study, difference in  $\overline{b}$  only appear when considering more than 160 networks (Extended Data Figure 4). Instead, most available studies use smaller datasets (e.g. 57 and 44 networks in<sup>4,53</sup>) because

they select networks with high sampling effort. Because sampling effort has consequences on  $S$  and  $L$ <sup>54,55</sup>, further studies should test its impact on  $b$ , even though it will be lower than the impact on connectance (because  $b$  is defined in the log-space). Across-network studies, in which the shape of the  $L \sim S$  relationship is computed based on  $\log(L) \sim \log(S)$  regression through multiple networks, have for example shown that low sampling effort tends to lead to scale invariance of  $L/S$  (i.e.  $L = \alpha \cdot S$ ) for intrinsically scale-dependent systems (i.e.  $L = \alpha \cdot S^2$ )<sup>56</sup>.

We connected our network-specific property  $b$  to the usual across-network regression (Supplementary Equation 3). When the variance of  $S$  is sufficiently large, the slope  $\beta$  of the across-network regression corresponds to the value of the network-specific  $b$  averaged across all networks ( $\bar{b}$ ). When  $\text{var}(S)$  is smaller, however,  $\beta$  also contains information about  $\text{cov}(b, S)$  and the distribution of  $S$ . The  $\text{cov}(b, S)$  can contain actual biological effects but also effects of sampling effort. This highlights the importance of using non-biased datasets when comparing  $\beta$ . Moreover, using the across-network regression only leads to significant difference between the two interaction types when large data sets are used (more than 200 networks). In contrast, the network-specific approach highlighted such differences in terms of  $\bar{b}$ ,  $\text{var}(b)$  and slope of the  $b \sim S$  relationship even in small datasets. Using a network-specific approach therefore extracts information that the across-network regression might overlook, while reliant on exactly the same data as the across-network approach. In addition, this approach echoes early work suggesting that the  $L \sim S$  relationship is not universal but might be community-specific<sup>15,22</sup> and change along temporal<sup>5,26,27</sup> and spatial gradients<sup>28–30</sup>.

Reinterpreting the  $L \sim S$  relationship as a network-specific property allowed us to identify a single parameter that summarizes how both  $L$  and  $S$  relate along gradient of sequential and random species removal. This parameter formally links community robustness and local stability. While more realism (e.g. rewiring, competitive links, non-random removal, or



interaction strengths) still need to be added to the framework, it elucidates the intricate relationships between network structure and stability in ecological communities. Moreover, because our approach is based on networks degree distribution, our results are expected to also hold for various type of scale-free networks<sup>57</sup> such as cellular, communication, or social networks (see Supplementary Equation 1 for a demonstration). The method presented here is therefore not restricted to ecological communities, and could be used to explore the relationship between structure and stability in a much broader class of real-world networks.

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## Author Contributions Statement

C. C. conceived the presented ideas, developed the theory and performed the analytic calculations and the *in-silico* experiments. G. B., J. W. S. and F. D. L. contributed to the analytical methods. F.D.L. and C.C. wrote the first version of the manuscript. All authors discussed the results and contributed to the final manuscript.

## Additional Information

**Supplementary Information** is available for this paper.

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## **Competing Interests Statement**

The authors declare no competing interests.

## Methods

### Empirical network dataset.

The empirical networks used in this study come from seven articles<sup>60–66</sup> and three databases: GlobalWeb (<http://globalwebdb.com>), Interaction Web Database (<https://iwebdb.nceas.ucsb.edu/>) and WebOfLife ([www.web-of-life.es](http://www.web-of-life.es)). Networks published before the 1990s were removed from the original dataset, as most of these were not designed to study network architecture and they have been described as poorly resolved, highly aggregated, and containing little diversity<sup>55,56,67</sup>. Furthermore, we excluded networks with potential errors (e.g.  $S$  and/or  $L$  not identical in publication and database). If networks appeared in multiple databases, only one copy was kept. We thereby obtained 435 networks: 186 trophic networks (110 food webs and 76 herbivory networks) and 249 mutualistic ones (229 pollination and 20 seed dispersal networks). Supplementary Data 1 contains the list of used networks. The number of species ranges from 5 to 266, with a median value of 35 (Extended Data Figure 6). The number of links ranges from 6 to 3584, with a median value of 58 (Extended Data Figure 6).

Each network is represented by its signed adjacency matrix  $A$ ; when species  $i$  and  $j$  interact, the elements  $a_{ij}$  and  $a_{ji}$  are set, respectively, to -1 and 1 in trophic networks and to 1 and 1 in mutualistic ones. When  $i$  and  $j$  do not interact,  $a_{ij} = 0$  and  $a_{ji} = 0$ . Cannibalism was not taken into account. The number of species ( $S$ ) is defined as the size (number of rows) of  $A$ ; the number of links ( $L$ ) is the number of edges in the network and, therefore, half the number of non-zero entries in  $A$ . Species with no interactions were removed from the original network.

### Network decomposition.

For each network, we performed *in-silico* extinction experiments by sequentially removing species: at each step of one decomposition process, one random species is removed from the network (primary extinction). A secondary extinction occurs when a non-independent species

loses all its resources or has no links left. Resources are prey in trophic networks and hosts in the mutualistic ones<sup>11</sup>. An independent species is defined as a species that might undergo primary extinction but does not undergo secondary extinction. The effect of independent species was tested by simulating network decomposition following two scenarios: in scenario 1, all species can undergo both primary and secondary extinction while scenario 2 assumes that a fraction  $z$  of species is independent. In this last scenario, independent species were the ones without any incoming links. In the mutualistic networks, the scenario 1 therefore represented a system where plants and animals are mutually dependent while, in scenario 2, we considered that plants do not depend on their partners for their persistence (e.g. they self-reproduce). In trophic networks, the scenario 1 assumed that predators are needed for the survival of the basal species while the scenario 2 hypothesised that these species persist after their predator extinction (extinctions cascade only to higher trophic level).

Because we assumed the independent species to be the ones without any incoming links, scenario 2 only impacts  $S$ : when a prey/plant has no predator/partner left, the fact that it stays or not in the network does not matter for the rest of the decomposition (because there is no rewiring) but only allows to maintain higher value of  $S$ . This holds true if the independent species are the ones without any outgoing links (e.g. top predators in trophic networks and animal in mutualistic ones).

We performed 10,000 simulations per scenario per network. The decompositions were stopped when there were no species left in the network. At each step of the decomposition, we computed the  $S$  and  $L$ .

### **Inferring the $L \sim S$ relationship.**

The network-specific  $L \sim S$  relationships were inferred based on 10,000 decompositions per network per scenario: for each network-scenario combination, we performed a linear least-

squares regression in the  $\log(L) \sim \log(S)$  space, leading to one value of  $a$ ,  $b$  and  $R^2$  per network (Extended Data Figure 1). The values presented in the Results are, therefore, the averaged  $\overline{R^2}$  across all networks (details in Extended Data Figure 1). The  $R^2$  obtained by regression were compared to the  $R^2$  obtained by Equation 1 (with  $b$  obtained from Equation 2) for each network (Extended Data Figure 1-2). The  $R^2$  of Equation 1 were also computed in the  $\log(L) \sim \log(S)$  space to allow comparison with the regression approach.

### **Performance of $\widehat{\Delta S}$ prediction.**

For each network and scenario, we compared the predicted number of species lost  $\sim$  removed relationship (Equation 3 with  $\widehat{\Delta S}$  based on Equation 4) to the relationship observed through the 10,000 *in-silico* experiment. This comparison led to an  $R^2$  for each network in each scenario: the  $\overline{R^2}$  presented in the result is the averaged  $R^2$  across all networks.

### **Robustness analysis.**

For each decomposition, we assess the number of species one needs to remove such that at least a fraction  $x$  of species is lost. The robustness  $Rob_x$  is then this number divided by the initial species richness and averaged over the 10,000 decompositions of each network and scenario. We also computed the variance of robustness across the 10,000 decompositions.

Because we assessed the robustness as the fraction of species to remove such that we exceeded the threshold  $x$ , we needed to consider the difference between the theoretically desired threshold  $x$  and the biologically realistic (effective) threshold  $x_{eff}$ . This difference arises because  $S$  is an integer. In a network composed of three species, for example, finding the robustness at  $x = 0.50$  requires finding how many species to remove such that we lose at least 1.5 species, which translates to the loss of 2 species. In this case  $x_{eff} = 2/3$  which corresponds to  $ceil(x \cdot S)/S$ , where  $ceil(\bullet)$  is the ceiling function. The difference between  $x$  and  $x_{eff}$  is small when  $S$  is



large but does matter when  $S$  is small. Therefore, the predicted  $Rob_x$  presented in the Results are based on Equation 5 adjusted by replacing  $x$  with  $\text{ceil}(x \cdot S)/S$ . Note that this way of measuring robustness might lead to its overestimation, with  $x$  being always  $\leq x_{eff}$ .

### **Computation of local stability.**

We created 1,000 community matrices ( $M$ ) for each empirical network in our database. Each matrix  $M$  is defined as  $M = W \circ A$ . Here,  $W$  is the interaction strength matrix,  $A$  is the adjacency matrix and  $\circ$  denotes the Hadamard (element-by-element) product of two matrices. As in Allesina and Tang<sup>2</sup>, the elements of  $W$  are drawn from a half-normal distribution  $|N(\mu, \sigma^2)|$ , with  $\mu = 0$  and  $\sigma^2 = 1$ . Because of this construction, pairwise interactions in  $M$  are correlated<sup>52</sup> with a coefficient  $\rho = -2/\pi$  in trophic networks and  $\rho = 2/\pi$  in mutualistic ones. Species' self-limitation terms (diagonal elements of  $M$ ) are set to  $d = 0$ . Note that setting another value for  $d$  would only shift the support of the eigenvalues on the complex plane (to the left if we lower  $d$  and to the right otherwise). Therefore, the value of  $d$  will not qualitatively impact the trade-off between local stability and robustness.

We computed the eigenvalues of  $W$  using the function *linalg.eig* from the *NumPy* library in Python and used the real part of the highest of these eigenvalues to infer matrix local stability (observed  $\Re(\lambda_{max})$ ). Reproducing this process for 1,000 community matrices per empirical network allows to compute the averaged  $\Re(\lambda_{max})$  and its variance for each of these networks.

### **Prediction of local stability.**

We predicted  $\Re(\lambda_{max})$  for each network based on random matrix theory<sup>2,3</sup>. As long as the number of species  $S$  is large, the real part of the rightmost eigenvalue of the community matrix  $M$  in the case of trophic networks can be obtained as<sup>2</sup>:

$$\Re(\lambda_{max}) = -d + \sigma \cdot \sqrt{S \cdot C} \cdot (1 + \rho)$$

Because connectance  $C$  in this equation is based on the number of non-zero entries in the community matrix,  $C$  equals  $2 \cdot L/S^2$  and therefore:

$$\Re(\lambda_{max}) = -d + \sigma \cdot \sqrt{2^{1-b} \cdot S^{b-1}} \cdot (1 + \rho)$$

$$\Re(\lambda_{max}) = -d + \sigma \cdot \sqrt{(S/2)^{b-1}} \cdot (1 + \rho) \quad (7)$$

This equation predicts  $\Re(\lambda_{max})$  of both food webs and herbivory networks: even though the latter are bipartite, the influence of their anti-modular structure is negligible because the networks of our database have comparable numbers of plants and animals, as explained with Supplementary Equations 4. Note that, for less well-balanced systems, Equation 7 would lead to an underestimation of  $\Re(\lambda_{max})$  and consequently to an overestimation of local stability.

In the mutualistic networks, however, the bipartite structure has a strong destabilizing effect (because  $\mu > 0$ ) and must, therefore, be considered separately. The adjacency matrix  $A$  of a bipartite network is divided into two systems (e.g. "plants" and "pollinators" in pollination networks) and species only interact between systems but not within them. This leads to a block-structure in  $A$  such that<sup>3</sup>:

$$A = \begin{pmatrix} 0 & Z \\ Y & 0 \end{pmatrix}$$

where  $Z$  is an  $\alpha \cdot S \times (1 - \alpha) \cdot S$  and  $Y$  is a  $(1 - \alpha) \cdot S \times \alpha \cdot S$  matrix ( $\alpha$  being the proportion of species belonging to the first system with,  $\alpha \leq 1/2$ ). This representation allows one to compute the eigenvalues of  $M$ : their support is estimated via a square-root transformation of the ellipse containing the eigenvalues of the matrix  $ZY$  - except for two outliers<sup>3,68</sup>. The  $\Re(\lambda_{max})$  is therefore given by (details in Supplementary Equations 4):

$$\Re(\lambda_{max}) = -d + \left( \frac{S \cdot C \cdot \mu}{2 \cdot \sqrt{\alpha \cdot (1 - \alpha)}} \right) + \frac{\rho \cdot \left( \sigma^2 + \left( 1 - \frac{C}{2 \cdot \alpha \cdot (1 - \alpha)} \right) \cdot \mu^2 \right)}{\mu \cdot \sqrt{\alpha \cdot (1 - \alpha)}}$$

The second term is proportional to  $S \cdot C \propto S^{(b-1)}$  while the third is proportional to  $C \propto S^{(b-2)}$ .

Therefore, for large  $S$ :

$$\Re(\lambda_{max}) \approx -d + \frac{(S/2)^{b-1} \cdot \mu}{2 \cdot \sqrt{\alpha \cdot (1 - \alpha)}} \quad (8)$$

## Statistical analyses.

Because the value of  $b$  is based on  $S$ , we need to test if the differences observed in the distribution of  $b$  between the two interaction types is not due to biased in either dataset. Therefore, we determined whether the distribution of  $S$  is the same in mutualistic and trophic networks, and whether the number of networks analysed impacted the results. To do so, we randomly drew  $\eta$  mutualistic and  $\eta$  trophic networks from our dataset (with  $\eta \in [20, 190]$  with a step of 10) and performed three statistical tests (Extended Data Figure 4): (1) we compared the distribution of  $b$  (and  $S$ ) in the drawn mutualistic and trophic networks through two-sample Kolmogorov–Smirnov tests; (2) we performed a Levene test to compare the variance of  $b$  (and  $S$ ) between the two types of networks; (3) we used an unequal variances  $t$ -tests (Welch  $t$ -tests) to compare their mean value of  $b$  (and  $S$ ). We also computed the slope of the relationship between  $b$  and  $S$  in the  $\eta$  mutualistic and  $\eta$  trophic networks (using linear regression) and the slope  $\beta$  of the across-network  $L \sim S$  relationship for these two types of networks (using log-log regression). To make sure the results were not due to a particular sampling of our dataset, we repeated this process 100 times per sample size  $\eta$ . This also allowed to test the normality of the distributions of the mean  $b$  and  $S$  (assumption of the Welch  $t$ -test) by performing a Shapiro test on the  $2 \cdot 100$  means computed for each sample size  $\eta$ . Moreover, we tested the difference between the slope between  $b$  and  $S$  in mutualistic and trophic networks using Welch  $t$ -tests on the  $2 \cdot 100$  values obtained per sample size  $\eta$  (because we worked with the  $2 \cdot 100$  values, the normality assumption of these Welch  $t$ -test was considered as fulfilled). Finally, we tested the

difference between the slope  $\beta$  of the log-log regression in mutualistic and trophic networks using Welch *t*-tests on the  $2 \cdot 100$  values obtained per sample size  $\eta$ .

To perform these analyses, we used the package SciPy in Python. The functions used were: *scipy.stats.ks\_2samp*, *scipy.stats.levene*, *scipy.stats.ttest\_ind* and *scipy.stats.linregress*.

## Data Availability

The empirical network matrices that support the findings of this study are available from seven datasets published on Dryad<sup>60–66</sup> and from three online databases:

- The GlobalWeb (<http://globalwebdb.com>) hosted by the University of Canberra (Canberra, Australia).
- Interaction Web Database (<https://iwdb.nceas.ucsb.edu/>) hosted by the National Center for Ecological Analysis and Synthesis (University of California, Santa Barbara, U.S.A.).
- This work has used the Web of Life dataset ([www.web-of-life.es](http://www.web-of-life.es)), a service created by Raúl Ortega, Miguel Angel Fortuna, and Jordi Bascompte and provided by the Bascompte Lab at the Spanish Research Council.

The empirical networks used are listed in Supplementary Data 1. This file also contains the metrics computed based on the *in-silico* experiments and the equations: these data allow the reproduction of Figure 2c, 3, 4 and 5.

## Code Availability

Code needed to reproduce the results presented in the article is available at Zenodo with the identifier <https://doi.org/10.5281/zenodo.4671579><sup>69</sup>.